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Abundance and survival rates of three leaf-litter frog species in fragments and continuous forest of the Mata Atlântica, Brazil

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Abstract

Habitat destruction and fragmentation alter the quality of habitats and put populations under the risk of extinction. Changes in population parameters can provide early warning signs of negative impacts. In tropical forests, where habitat loss and fragmentation are vast, such indicators are of high relevance for directing conservation efforts before effects are irreversible. Most of our knowledge from tropical ecosystems originates from community level surveys, whereas our understanding of the influence of habitat conversion on vital rates of species is limited. This study focused on the influence of anthropogenic habitat fragmentation on the survival probability and abundance of three leaf-litter frog species (*Rhinella ornata*, *Ischnocnema guentheri* and *I. parva*) in forest patches of the Atlantic rainforest of South-east Brazil compared to a continuous forest. The species differ in their matrix tolerance: high for *R. ornata* and low for *I. guentheri* and *I. parva* and, thus, we examined whether their survival and abundance correspond to this classification. *Ischnocnema guentheri* showed highest abundances in all study sites and low mortality in the forest patches compared to the continuous forest; *I. parva* was encountered only in isolated fragments, with very low mortality in one isolated fragment; and the matrix tolerant species had generally low abundance and showed no clear pattern in terms of mortality in the different sites. Our counter-intuitive results show that even matrix sensitive amphibian species may show high abundance and low mortality in

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small forest patches. Therefore, these patches can be of high value for amphibian conservation regardless of their degree of matrix aversion. Landscape level conservation planning should not abandon small habitat patches, especially in highly fragmented tropical environments.

Keywords
Amphibia, Brazilian Atlantic Forest, habitat fragmentation, abundance, mark-recapture, survival

Introduction

Habitat destruction and fragmentation are amongst the major causes for the loss of terrestrial biodiversity (Saunders et al. 1991, Pimm and Raven 2000, Laurance and Cochrane 2001, Henle et al. 2004a). Besides loss of suitable area and isolation of remaining habitats, the fragmentation process may result in changes of habitat geometry and the physical environment, thus influencing habitat quality parameters both directly (Lovejoy et al. 1986, Saunders et al. 1991, Laurance 2000, Fahrig 2003) and indirectly, e.g. through edge effects (Murcia 1995, Ewers and Didham 2006). This in turn can influence individual traits (Steinicke et al. 2015) as well as the extinction risk of populations and the composition of communities within patches (Saunders et al. 1991, Davies et al. 2001, Wiegand et al. 2001, Hokit and Branch 2003, Ewers et al. 2007, Zurita et al. 2012). Together, loss and change of the quality of habitats and isolation of remaining patches affect the persistence of species in fragmented landscapes (Settele et al. 1996, Halverson et al. 2006, Watling and Donnelly 2007).

Whether a species in a fragmented habitat is vulnerable to extinction or not, depends not only on the spatial configuration of the landscape (Gunton et al. 2017), but also on demographic parameters and on the ecological traits of species (With and Crist 1995, Henle et al. 2004a). Species with narrow habitat requirements, i.e. habitat specialists, are likely to be more affected than habitat generalists, as the chance that their niche is represented in remnants of a fragmented landscape is smaller (Henle et al. 2004a). Habitat specialists also often exhibit lower tolerance to the matrix surrounding the remnants (Gascon et al. 1999, Bentley et al. 2000, Henle et al. 2004a, Hoehn et al. 2007) and therefore they are considered to be more prone to extinction than habitat generalists (Sarre et al. 1996, Henle et al. 2004a).

Tropical forest species are often assumed to be more sensitive to fragmentation than temperate ones (Henle et al. 2004a), partly due to their high specialisation levels. Habitat loss and fragmentation are particularly severe in tropical forests. The Brazilian Atlantic Forest (Mata Atlântica) is one of the global biodiversity hotspots severely impacted by habitat loss and fragmentation. Only 11-16% of its original area remains wooded with native forests and these remnants are highly fragmented, isolated and disturbed to an extent where many of them only retain intermediate secondary forest (Oliveira and Fontes 2000, Ribeiro et al. 2009). Despite its severe fragmentation, the Mata Atlântica still maintains high species richness, including a large number of en-

demic species (Tabarelli et al. 2005), with particularly high endemism of amphibians (Myers et al. 2000, Haddad et al. 2013).

Compared to the temperate zone, much less is known about the effects of fragmentation on amphibians from tropical forest ecosystems. As for the majority of fragmentation studies in tropical forests, the available studies for amphibians focus primarily on the community level or genetic variability (e.g. Pineda and Halffter 2004, Bell and Donnelly 2006, Dixo et al. 2009, Lion et al. 2014, Riemann et al. 2015, Almeida-Gomes et al. 2016). Existing studies have revealed differences amongst amphibian taxa in response to habitat fragmentation (Almeida-Gomes et al. 2016), finding that ground-living species (Pineda and Halffter 2004), naturally rare species and species with a high habitat specialisation are more affected than others (Gascon et al. 1999, Watling and Donnelly 2007, Almeida-Gomes et al. 2016). Sensitivity to fragmentation may further depend on their reproductive mode and the proximity of water bodies to the forest patches but results obtained so far are not consistent (Cannatella 2008, Bickford et al. 2010, Lion et al. 2014, Almeida-Gomes et al. 2016).

Effects of fragmentation on the survival of species are governed by changes in demographic processes. However, knowledge about demography in relation to habitat fragmentation is scarce (but see e.g. Funk and Mills 2003, Holland and Bennett 2010), especially in tropical regions (e.g. Freitas et al. 2003). For amphibians, in general, few studies have assessed the population dynamics of tropical species (but see Funk and Mills 2003, Grafe et al. 2004, Ryan et al. 2008, McCaffery and Lips 2013). Thus, for a better understanding of the persistence of species in fragmented landscapes, information on population dynamics should receive top priority in tropical ecological research (Bierregaard et al. 1997).

This study aims to address this still existing gap in ecological knowledge. We studied the abundance and mortality of three leaf-litter amphibian species, differing in their level of matrix tolerance, in forest fragments and in a comparable site of continuous forest in the Brazilian Atlantic Forest in south-eastern Brazil.

Our focus on abundance and mortality stems from the assumption that population size and fluctuation are two key factors determining whether species are able to maintain stable populations or are prone to stochastic extinction (Henle et al. 2004a, Henle et al. 2004b). Therefore, these population parameters can serve as important early warning signs, potentially indicating a pending extinction debt (McCarthy et al. 1997, Kuussaari et al. 2009), whereas abundance data alone are insufficient to detect such trends. For instance, van Strien et al. (2011) showed that metapopulation dynamics may change some tens of years before an actual change in occupancy is visible. Additionally, mortality rates may aid in identifying whether species observed in a fragmented landscape perform better in non-fragmented than in fragmented habitats. As habitat specialists tend to be more fragmentation-sensitive than generalists, we expected that the relative performance would reflect the degree of matrix tolerance of the three leaf-litter frog species studied by us. We discuss the role of small fragments for the conservation of Neotropical leaf-litter frog species.

Material and methods

Study area

We carried out our study on the Atlantic Plateau of São Paulo in the Mata Atlântica of Brazil at an altitude of 860–1075 m above sea level (Metzger et al. 2006). The study region comprised a continuous forest area at the Morro Grande Reserve, approx. 10,000 ha in size and a neighbouring fragmented landscape (Figure 1) surrounding Caucaia do Alto (23°40'S; 47°01'W) in the municipalities of Cotia and Ibiúna, 40 km southwest of São Paulo. Oliveira and Fontes (2000) classified the original forest as lower montane rainforest that forms a transition between the coastal Atlantic rain forest and the Atlantic semi-deciduous forest. The fragmented landscape comprises 31% secondary forest cover, 39% open areas (mainly agricultural and pasture), 17% tree plantations (mainly *Eucalyptus* and pine plantations) and 15% human settlements (Uezu et al. 2005, Metzger et al. 2006, Dixo et al. 2009). In both the continuous landscape and the fragmented one, primary forest has almost completely disappeared due to historical clear-cuts followed by regeneration. Mature forest ages are estimated between 60 and 80 years (Metzger et al. 2009).

We selected four study sites: one control site within the continuous forest of the Morro Grande Reserve ("control"), one small fragment (Alcides), 5 ha in size, which is connected by a corridor to a larger forest area ("connected") and two small isolated patches, 5 ha each. One of the latter (Carmo Messias) is surrounded by a mixture of habitats including riparian habitat, ("isolated 1"), the other (Dito) is close to a settlement and its only neighbouring forest patches are small and degraded ("isolated 2"; Table 1). All sites are characterised by secondary forest that has not experienced major logging or disturbance for at least 60 years. All studied forest patches and the site in the continuous forest were devoid of permanent/large water bodies within the forest area or within a radius of 200 m from the forest patches or within that distance to any of the survey sites.

Selected species

Based on capture numbers from Dixo (2005), we chose three leaf-litter dwelling, forest species that were expected to be sufficiently abundant for a capture-mark-recapture study in all sites: *Rhinella ornata* (Spix, 1824; Bufonidae), *Ischnocnema guentheri* (Steindachner, 1864; Brachycephalidae) and *Ischnocnema parva* (Girard, 1853; Brachycephalidae). All three species are listed as of "Least Concern" (IUCN 2013). We classified the three species according to their tendency to tolerate or avoid the surrounding agricultural matrix as elaborated in the following.

Of the three species, *R. ornata* is the most tolerant to the agricultural matrix. It can be found in undisturbed continuous forest as well as in disturbed forest fragments (Heyer et al. 1990, Dixo 2005). It migrates to temporary and permanent ponds within

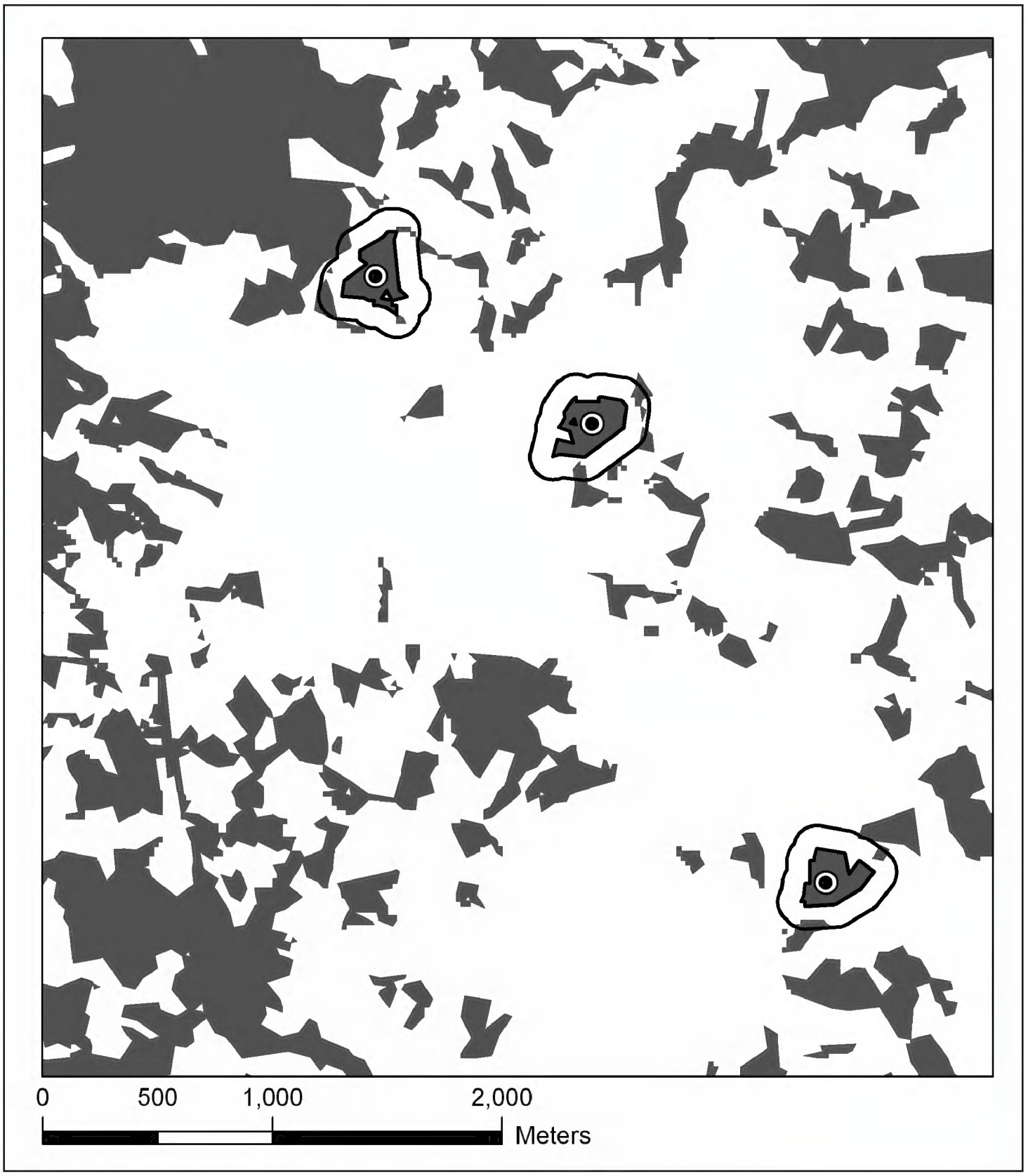

Figure 1. Map of the study area. Circles around the patches represent buffers of 100 m to assess the level of isolation in terms of forest patches within a reachable distance (see Table 1). Patches are from north to south "connected", "isolated 1" and "isolated 2".

forests and open areas for breeding (Izecksohn and de Carvalho-e-Silva 2001, Haddad and Prado 2005). Reproduction starts at the end of the dry season in late July or the beginning of August (Dixo 2005). It is distributed throughout the Atlantic Forest from Espírito Santo in the north to Paraná in the south (Frost 2017).

Ischnocnema parva is the least matrix tolerant of the three species, not only avoiding the external matrix but also forest edges (Heyer et al. 1990, IUCN et al. 2006). Females deposit egg clutches terrestrially and development is directly within egg capsules

Table 1. Characterisation of the study sites. Habitats around each study site are ordered according to ranking of border-length. Forest cover within 100 m represents the area of forest within a buffer of that distance, whilst the total area of forest patches represents the total area of all patches that partly or fully occur within this buffer.

	Patch size	Habitats neighbouring the site	Distance to nearest patch	Forest cover within a 100 m buffer / Total area of forest patches
control	Continuous forest			
connected	5.11 ha	Open, plantation, riparian, corridor, settlements	Connected by corridor	67.4 / 203.25 ha
isolated 1	5.41 ha	Settlement, open, plantation	20 m	0.37 / 2.65 ha
isolated 2	4.88 ha	Open, riparian, plantations	43 m	1.44 / 4.35 ha

(Heyer et al. 1990, Izecksohn and de Carvalho-e-Silva 2001, Haddad and Prado 2005). Reproduction occurs between October and December. It is distributed in the southeast of the Mata Atlântica; the populations in the state of São Paulo may be an undescribed cryptic species (Frost 2017).

In terms of matrix tolerance, *I. guentheri* is positioned between the other two species. It occurs primarily within forest habitats but has been found, albeit very rarely, in cleared and degraded areas (Heyer et al. 1990) and it also occurs at the forest edge (HS and KH pers. observ. in the study area). Females deposit egg clutches terrestrially, hidden below tree trunks and stones (Kwet and di-Bernardo 1999, Izecksohn and de Carvalho-e-Silva 2001). Frogs develop directly within the egg capsule (Heyer et al. 1990, Izecksohn and de Carvalho-e-Silva 2001). Reproduction occurs between August and December (Heyer et al. 1990). The *I. guentheri* species group is distributed over large parts of the Mata Atlântica; the populations in the state of São Paulo may be an undescribed species (Frost 2017).

Both *I. guentheri* and *I. parva* are assumed to be territorial species that do not migrate over long distances, but data on individual movement behaviour are scarce.

Sampling

We sampled frogs by hand along three parallel transects, 100 m each in each study site (meaning that, in the fragments, most of the patch excluding the edge was covered). We performed sampling during two rainy seasons, from October 2003 until March 2004 and November 2004 until March 2005. We implemented a robust design of mark recapture studies (Pollock 1982), surveying each site for five consecutive nights (21:00-01:00 h local time) (hereafter, 'secondary periods') before sampling the next site. Once all sites had been sampled, the next round of sampling started again at the first site. In total, we conducted five sampling rounds. These five sampling rounds serve as 'primary periods', each containing the five consecutive nights per site as 'secondary periods'. Thus, the total search effort was 25 nights per site (15 nights per site in 2003/2004 and 10 nights per site during 2004/2005).

We photographed all body sides of all captured animals using a digital camera with a macro lens and a flash bulb and used pattern for individual identification (Donnelly et al. 1994, Henle et al. 1997). Once photographed, we released each animal at the point of capture.

Data analysis

Due to low recapture rates within primary periods, we used the number of individuals captured within a primary period as a measure of relative abundance. For the survival analysis, we combined all captures from the secondary sampling periods of a primary sampling period to analyse survival probabilities between primary periods. We calculated local survival probabilities (φ) and capture probabilities (p) using programme MARK (White and Burnham 1999). Local survival is defined as the probability of an individual to survive and remain on the study site from one primary capture period to the next. As periods between primary sessions differed, we standardised the parameters in terms of weekly survival rates.

We fitted several candidate Cormack-Jolly-Seber models to the recapture data to determine the most parsimonious model (Table 2). We used the notation of Lebreton et al. (1992) for model specification. Following the recommendation of Burnham and Anderson (2001), we chose the set of candidate models *a priori*. The most general model we used assumed time specific survival and capture probabilities [$\varphi(t)$; $p(t)$]; the most restrictive one assumed constant survival and constant capture probabilities [$\varphi(.)$; $p(.)$]. The model selection in MARK is based on the corrected Akaike Information Criterion (*AICc*) (Hurvich and Tsai 1989), an adjustment for the *AIC* for small sample sizes and overdispersion (Buckland et al. 1997). Models with a $\Delta AICc \leq 2.0$ are usually regarded as equally parsimonious. If $\Delta AICc$ was less or equal to this value, then we selected the more restrictive model representing time-independent estimates.

To determine whether estimated survival probabilities differed significantly between study sites, we calculated log-based 85% confidence intervals and checked for overlap. Non-overlap of 85% confidence intervals is equivalent to a 5% significance level in a two-sided test ($\alpha \leq 0.05$) (Buckland et al. 1993).

Results

Abundances

In total, we captured 632 individuals of the three focal species at least once, representing 116 individuals of *R. ornata*, 383 individuals of *I. guentheri* and 133 individuals of *I. parva*. *Rhinella ornata*, the most matrix tolerant species, was more abundant in the isolated patches and less abundant in the connected patch and in the control site (Figure 2). *Ischnocnema guentheri* was most abundant in the isolated patches, less abundant in the

Table 2. Overview of models considered and results of model selection based on the corrected Akaike Information Criterion (AIC_c) for estimating survival probability (φ).

	Model tested	AIC_c	ΔAIC_c	AIC_c weight
control	*R. ornata*			
	φ(t) p(t)	5.439	0.000	0.851
	φ(t) p(.)	9.173	3.733	0.132
	φ(.) p(.)	13.234	7.795	0.017
	φ(.) p(t)	43.479	38.040	0.000
	I. guentheri			
	φ(t) p(t)	18.569	0.000	0.560
	φ(.) p(.)	19.829	1.261	0.298
	φ(t) p(.)	21.363	2.794	0.138
	φ(.) p(t)	28.657	10.089	0.004
connected	*I. guentheri*			
	φ(.) p(t)	35.455	0.000	0.846
	φ(.) p(.)	40.068	4.614	0.084
	φ(t) p(t)	41.250	5.795	0.047
	φ(t) p(.)	42.695	7.240	0.023
isolated 1	*R. ornata*			
	φ(.) p(.)	45.443	0.000	0.890
	φ(.) p(t)	50.137	4.694	0.085
	φ(t) p(.)	53.303	7.860	0.020
	φ(t) p(t)	55.103	9.660	0.007
	I. guentheri			
	φ(t) p(t)	145.685	0.000	0.607
	φ(t) p(.)	146.589	0.904	0.386
	φ(.) p(.)	154.716	9.031	0.007
	φ(.) p(t)	161.432	15.747	0.000
isolated 2	*R. ornata*			
	φ(.) p(.)	10.624	0.000	0.528
	φ(t) p(.)	12.345	1.721	0.223
	φ(t) p(t)	12.345	1.721	0.223
	φ(.) p(t)	16.649	6.024	0.026
	I. guentheri			
	φ(.) p(t)	70.224	0.000	0.699
	φ(.) p(.)	73.019	2.795	0.173
	φ(t) p(t)	73.927	3.702	0.110
	φ(t) p(.)	77.454	7.230	0.019
	I. parva			
	φ(t) p(.)	97.256	0.000	0.466
	φ(t) p(t)	98.058	0.802	0.312
	φ(.) p(t)	98.823	1.567	0.213
	φ(.) p(.)	105.087	7.830	0.009

connected patch and had the lowest abundance at the control site (Figure 2). The least matrix tolerant species, *I. parva*, was only captured in the isolated patches, mainly in the most isolated study site "isolated 2", but was neither captured in the "connected" fragment nor in the "control" site.

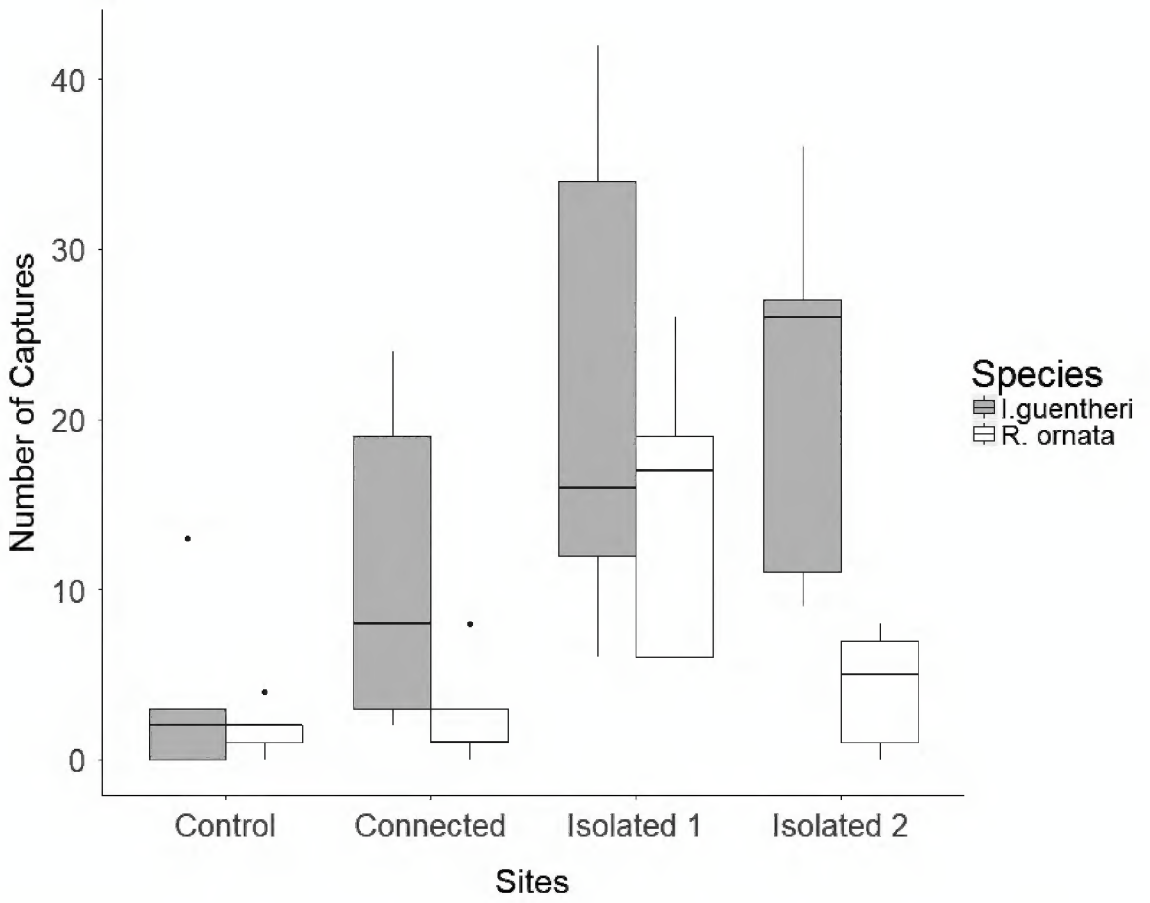

Figure 2. Comparison of the number of captures of *Rhinella ornata* and *Ischnocnema guentheri* in the study sites. The median, first and third quartile, minimum-maximum range and outliers of capture rates are indicated.

The number of captures per primary period of *R. ornata* tended to be larger in all fragments compared to the control site and of *I. guentheri* in the isolated sites compared to the control site. However, the difference between the control site and any of the three fragments was not significant for both species, likely due to low power associated with the small number (5) of primary periods (Wilcoxon test with Bonferroni correction: $\alpha > 0.05$ for both species).

Survival

The number of animals captured allowed the calculation of survival probabilities for *R. ornata* for all sites except for the "connected" fragment, for *I. guentheri* at all study sites and for *I. parva* only for the fragment "isolated 2". For all but two cases (*R. ornata* at the "control" site and *I. guentheri* at the "isolated1" patch), models with time-independent survival yielded the lowest *AICc* or rendered a $\Delta AICc$ within the threshold and were therefore used for parameter estimation. In the two exceptions, the *AICc* values suggested time-dependent models of survival but they had uninformative large confidence intervals due to seasonally poor recapture rates. Therefore, we also provide results from time-independent survival models for these two cases.

The estimated local survival probabilities of *R. ornata* were high for "isolated 1" ($\varphi = 0.99$) and the "control" site ($\varphi = 0.94$), but relatively low for "isolated 2" ($\varphi = 0.68$),

Table 3. Summary of the results of survival estimates in the different study sites.

Species	Selected model	Survival estimate	Standard error	95 % (85 %) Confidence interval	
				lower	upper
Control					
R. ornata	φ(.) p(.)	0.938	0.117	0.228 (0.455)	0.998 (0.996)
I. guentheri	φ(.) p(.)	0.726	0.132	0.418 (0.504)	0.907 (0.874)
Connected					
I. guentheri	φ(.) p(t)	0.933	0.015	0.898 (0.909)	0.957 (0.951)
Isolated 1					
R. ornata	φ(.) p(.)	0.992	0.023	0.289 (0.649)	0.999 (0.999)
I. guentheri	φ(.) p(.)	0.979	0.010	0.947 (0.959)	0.992 (0.990)
Isolated 2					
R. ornata	φ(.) p(.)	0.676	0.121	0.415 (0.485)	0.860 (0.822)
I. guentheri	φ(.) p(t)	0.927	0.012	0.901 (0.908)	0.947 (0.943)
I. parva	φ(.) p(t)	0.974	0.013	0.931 (0.946)	0.991 (0.988)

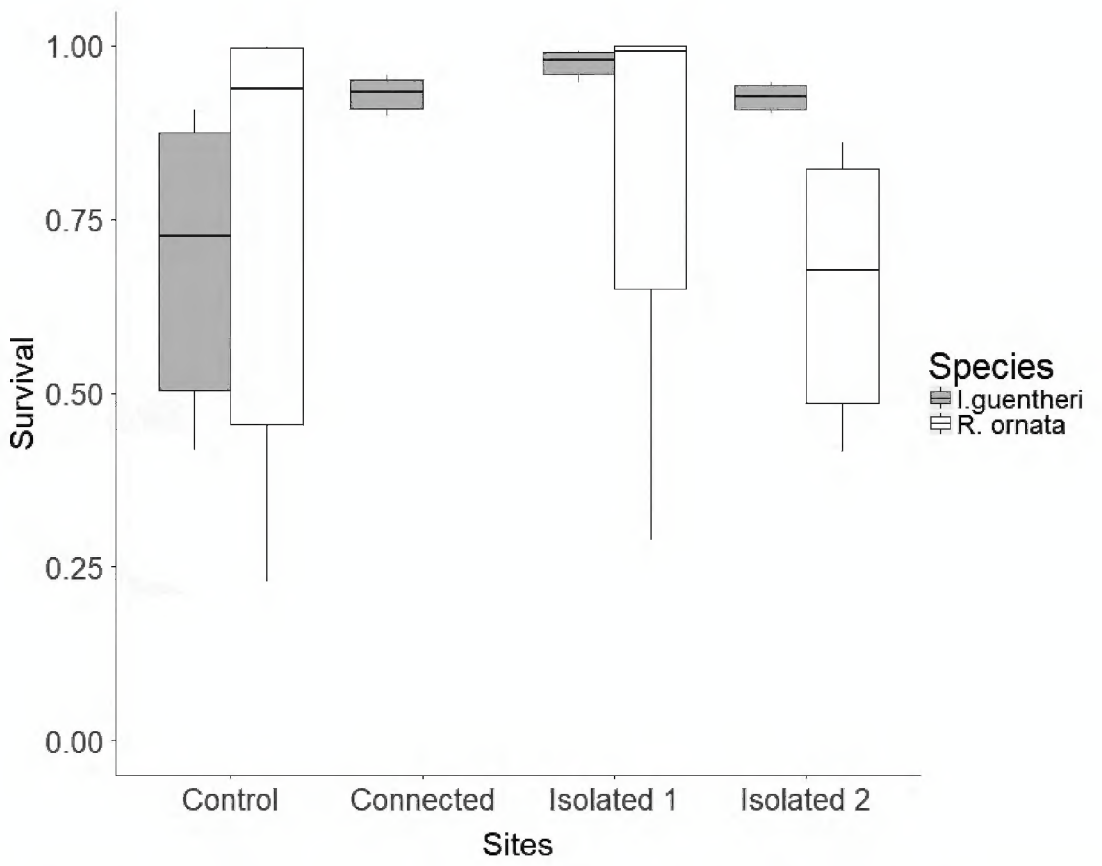

Figure 3. Comparison of weekly survival probability estimates φ of *R. ornata* and *I. guentheri* at the study sites. Data of *R. ornata* in the "connected" site were not sufficient for estimation. The survival estimate, upper and lower 85% confidence intervals (boxes) and the upper and lower 95% confidence intervals are indicated (minimum and maximum lines).

but, due to the large confidence intervals, the estimates were not significantly different (Table 3, Figure 3). Survival probabilities of *I. guentheri* were high in all three patches compared to the control site with a significantly higher value in "isolated 1" (Table 3, Figure 3). The most specialised species *I. parva* proved to have a very high survival probability in the patch "isolated 2". In fact, in this fragment, *I. parva* was the species with the highest survival probability (Table 3).

Discussion

General discussion

Forest fragmentation reduces habitat availability, increases edge effects and leads to the isolation of subpopulations from each other (Saunders et al. 1991, Laurance 2000, Fahrig 2003). The combined effect of reduced patch size and quality is known to negatively affect the abundance and survival rates of populations (Marsh and Pearman 1997, Hokit and Branch 2003, Henle et al. 2004a) and to alter trophic chains and species communities in forest fragments (Henle et al. 2004a). The reduction of habitat generally leads to a stronger reduction of possible niches for specialists compared to generalist species (Sarre et al. 1996, Henle et al. 2004a, Kimmel et al. 2010). Furthermore, increased edge effects are known to cause changes in microhabitat quality inside forests (Saunders et al. 1991), which affects forest specialist species particularly strongly (Laurance 2000). The isolation of remnants also leads to the isolation of populations, which may negatively affect survival rates (Halverson et al. 2006, Watling and Donnelly 2007). Highly specialised species therefore do often vanish with habitat fragmentation (Saunders et al. 1991, Laurance 2000). Less specialised species may persist in fragmented landscapes but with lower abundance, may exhibit source-sink dynamics or show negative trends over longer terms, eventually leading to their extinction (i.e. extinction debt). Alternatively, they may be pre-adapted to the changed ecological conditions in fragmentation or may hold the flexibility to adapt alternative strategies or habitat usage that may enable them to sustain populations in the long run.

As our studied species are all forest specialists, we anticipated all of them to exhibit negative effects of fragmentation, especially in the small and isolated forest patches. We further expected a ranking of the strength of response amongst the three species, where the most matrix intolerant species, *I. parva*, should exhibit the strongest response and thus lower abundance and/or local survival rate in the fragments compared to the control area.

Our results therefore seem counter-intuitive at first sight. *I. parva*, the species, which could be expected to be most sensitive to fragmentation and patch isolation as it avoided the forest edge, was found neither in the continuous forest site nor in the connected fragment, but only in isolated patches, in which it showed a very high survival probability. The abundance of the most matrix tolerant species, *R. ornata*, was near-significantly higher in the "isolated 1" fragment than at the control site, with no consistent pattern with respect to its survival in the different sites. The intermediate species in terms of matrix tolerance, *I. guentheri*, that tolerates forest edges and has been found, albeit very rarely, just within the matrix, did not show significant changes in abundance between the different fragments, had its lowest abundance in the continuous forest site and exhibited significantly higher survival probabilities in the forest fragments. Likewise, in an experimental fragmentation study in central Amazonia, survival in *Anomaloglossus stepheni* (as *Colostethus stepheni*) was not related to fragmentation (Funk and Mills 2003).

These results clearly demonstrate that the ranking order of species according to their matrix tolerance does not explain the trends from a continuous forest to the most isolated patch, as the small forest fragments did provide sufficient suitable habitat to host stable populations for all three species, even the most matrix intolerant one. Bickford et al. (2010) obtained similar results for anurans in rainforest fragments in Singapore, in which abundance was not related to fragment size or isolation.

For species that are less tolerant to the matrix, matrix-avoidance and low permeability of the matrix leads to a decrease in the exchange of individuals (Hanski 1991, Saunders et al. 1991, Fahrig and Merriam 1994, Gascon et al. 1999, Rosenberg et al. 1997, Hoehn et al. 2007). This consequently enhances inbreeding (Madsen et al. 1996) and potentially reduces survival due to inbreeding depression (Brook et al. 2002, Halverson et al. 2006), though increased intra-patch mobility may (partially) compensate for these effects (Lange et al. 2013). Likewise, an increase in available resources may lead to an increased abundance of leaf litter amphibians, as the abundance of leaf-litter invertebrates often increases in tropical forest fragments and as they are important prey for leaf-litter amphibians (e.g. Whitfield and Donnelly 2006).

In addition, the disappearance of predators that are sensitive to fragmentation can lead to a higher abundance and survival probability of species less sensitive to fragmentation (Terborgh 1974, Ogle 1987, Henle et al. 2004a) as was the case for *I. guentheri* in our study. Ants, spiders, snakes, mammals and especially understorey birds (such as obligatory ant-followers) are amongst the main predators of tropical leaf-litter anurans (McCormick et al. 1982, Poulin et al. 2001, Toledo et al. 2007). These groups are known to be sensitive to the fragmentation of tropical forests (Stouffer and Bierregaard 1995, Harrison and Bruna 1999, Vasconcelos et al. 2006). Their disappearance in fragmented landscapes and especially from small isolated patches is well-documented in the Mata Atlantica (Zurita et al. 2006, Zurita and Bellocq 2010), including the studied landscape (Uezu et al. 2005, Martensen et al 2008, Banks-Leite et al. 2010).

We must add one note of caution. Low mortality in small patches does not necessarily mean more stable populations compared to a continuous forest, since the lower local survival in the latter could also be due to higher emigration rates away from the sampled area, especially for the edge and matrix intolerant species, *I. parva* and *I. guentheri*. While in the small and isolated patches one can assume relatively closed populations, this assumption may not hold in a continuous environment and we cannot separate the two without tracking the movement of individuals.

Implications for conservation

Our findings support recent studies, indicating that small habitat patches can have an important conservation value (Bickford et al. 2010, Lion et al. 2016). This is especially true for taxonomic groups with limited spatial requirements that may also benefit from the absence of predators. In the case of temperate wetlands, there is evidence that even small isolated habitat patches can have a high value for sustaining

amphibian diversity (Semlitsch and Bodie 1998, Riemann et al. 2015). Tscharntke et al. (2002) reached similar conclusions for herbivorous insects and Ogle (1987) for endemic carnivorous snails in New Zealand forests. Our results and those of Bickford et al. (2010) concur with these findings for small fragments in a tropical forest. Our study further concurs with recent studies that point to mosaic landscapes as important for protection of species under fragmentation. Such heterogeneous landscapes maintain complementary elements and, combined with a benign management (which is often typical in rural landscapes), could support high species richness (Haslem and Bennett 2008, Norris 2008, Ranganathan et al. 2008) provided they retain all essential resources, such as suitable water bodies or terrestrial breeding sites for tropical amphibians. Though certainly less valuable than large continuous tropical forests, the heterogeneity of such landscapes should be maintained and protected from further intensification and degradation in order to safeguard biodiversity in face of habitat loss and fragmentation.

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